MODE OF GROWTH OF THE LOWER VERTEBRATES.

BY A. S. PACKARD, JR.

In the adult Amphioxus, we behold a vertebrate without a true back bone, but a dorsal cord like that of certain larval Ascidians; with no brain, no true heart, but with a vascular system resembling that of worms; with primitive kidneys like the segmental organs of worms, and with the front end of the alimentary canal perforated with gill-slits, like those of Ascidians and the Balanoglossus worm rather than vertebrates. Viewing the body externally, it has no true head as in fishes, nor appendages supported by bony axes, like the fins and arms or legs of vertebrates. Yet on making a section of the body, the relation of the chief anatomical organs is on the vertebrate plan, a nerve-cavity being situated above the digestive cavity, the vicarious back bone, or *chorda dorsalis*, separating the two cavities.

Development of Amphioxus. Again when we study the development of Amphioxus, we shall find, that while there are important points in which the embryology of this animal differs much from that of the higher vertebrates; still, as observed by Balfour, "all the modes of development found in the higher vertebrates are to be looked upon as modifications of that of Amphioxus."

For the life-history of the lancelet, we turn to Kowalevsky's classical memoir. He found the eggs issuing in May from the mouth of the female, and fertilized by spermatic particles likewise pouring out from the mouth of the male. The eggs are very small, 0.105 millimetres in diameter. The eggs undergo total segmentation, exactly as in the sponge, the ascidian, the mammal, and even as in man, and leaving a segmentation cavity which becomes the body-cavity.

The blastoderm now invaginates and the embryo swims about as a ciliated gastrula, comparable with that of the sponge, or Sagitta (Fig. 179). The body is now oval, and the germ does not differ much in appearance from a worm, starfish, snail or ascidian in the same stage of growth. No vertebrate features are yet developed.

Soon the lively ciliated gastrula elongates, the alimentary tube arises from the primitive gastrula-cavity, while the edges of the

flattened side of the body grow up as ridges which afterwards, as in all vertebrate embryos, grow over and enclose the spinal cord. By this time the transverse muscular bands appear.

By the time the embryo is twenty-four hours old it assumes the form of a ciliated flattened cylinder, with both ends much alike. It is now somewhat like the Ascidian embryo (Fig. 217, *B*, *n*), there being a nerve-cavity, the nerve-tube, with an external opening, which afterwards closes.

The vertebrate character, namely, the embryonic back bone (*chorda dorsalis*) has now appeared, and extends to the front end, beyond the end of the brain, instead of being confined to the posterior portion of the body as in the Ascidians (Fig. 217, *B*, *x*).

In the next stage observed by the Russian embryologist, the Amphioxus-form was attained, the body being compressed and deeper in the region of the mouth, though there is no true head. The first gill-opening now appears, the mouth having previously been formed, and afterwards twelve such openings appear; the pharynx is thus provided with ciliated slits, as in the ascidians, the Balanoglossus; and, on the other hand, all embryo vertebrates. The embryo lancelet is still ciliated, but these swimming-hairs disappear eventually and the young animal seeks the bottom and burrows finally in the sand. When the larval Amphioxus is still very small, the body is not symmetrical, the mouth is far on one side, and on the lower edge is a circle of external filaments surrounding the mouth, comparable with those of the ascidians, the clam or certain worms.

It seems to result from these and other facts, not here presented, that while the Amphioxus is a low, embryonic vertebrate, which graduates into the fishes through the lamprey and myxine, the early history of Amphioxus unmistakably points back to worm-like parents; and on the other hand that of the vertebrates indicates their descent from an Amphioxus-like ancestor.

Briefly recapitulating the chief events in the life of the lancelet, we find the following well marked stages:

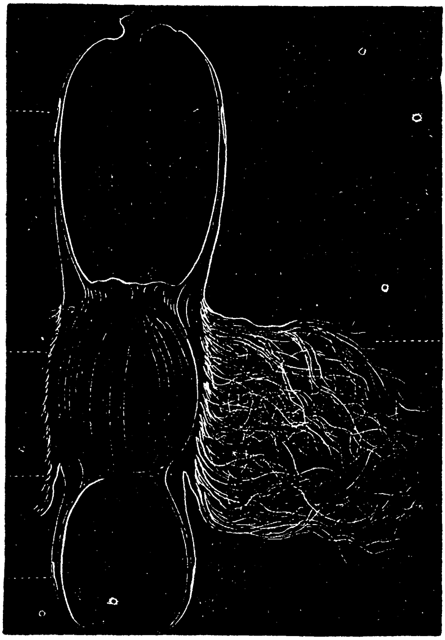
1. Morula.
2. Gastrula (ciliated).
3. Ascidian-like larva.
4. Adult.

LITERATURE.

Kowalevsky. Entwickelungsgeschichte des Amphioxus lanceolatus. (Memoires de l'Acad. Imp. des Sciences de St. Petersbourg, 1867).

Development of the Sharks and Skates (*Selachians*). These fishes are either oviparous or viviparous. The dog-fish brings forth her young alive, while the skates and many sharks lay square eggs like those of the skate (Fig. 285, after Wyman), each corner sending out a tendril by which it is attached to sea-weeds. The yolk is not enclosed in any membrane like the vitelline membrane of birds, but lies freely in a viscid albumen filling the egg-capsule (Balfour).

Fig. 285.

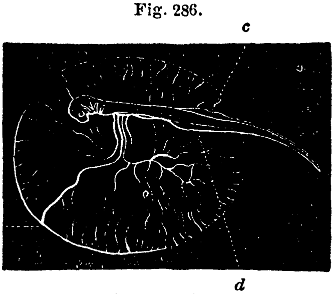


Egg of the Skate.

We will now, in order to make out a tolerably complete life-history of a Selachian, condense Balfour's account of the early stages of the dog-fish (Mustelus), and close with the latter stages of the skate, as given by the late Professor Wyman. The blastoderm or germinal disk is a large round spot darker than the rest of the yolk and marked off from the rest of the yolk by a dark line (really a shallow groove). Segmentation occurs much as described in the bony fishes, reptiles and birds. The upper germ-layer (epiblast) arises much as in the bony fishes, the Batrachians and birds, while the two inner germ-layers are not clearly indicated until a considerably later stage. The segmentation-cavity is formed much as in the bony fishes. There is no invagination of the outer germ-layer to form the primitive digestive cavity and anus of Rusconi, as in Amphioxus, the Lamprey, sturgeon and Batrachians, but the Selachians agree with the bony fishes, the reptiles and birds, in having the alimentary canal formed by an infolding of the innermost germ-layer, and with no anus of Rusconi, the digestive canal remaining

in communication with the yolk for the greater part of embryonic

Fig. 286.



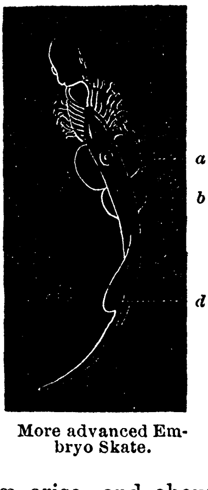
Embryo Skate.

life by an umbilical canal. This mode of origin of the digestive cavity, Balfour regards as secondary and adaptive, no "gastrula" (Hæckel) being formed as in Amphioxus, etc. The embryo now rises up as a distinct body from the blastoderm, just as in other vertebrates, and there is a medullary groove along the middle line, and by the time this has appeared the middle and inner germ-layers are closely indicated. And now development goes on much as in the chick.

At this time the embryo dog-fish externally resembles the young trout; the chief difference is an internal one, the outer germ-layer not being divided into a nervous and epidermal sub-layer as in the bony fishes.

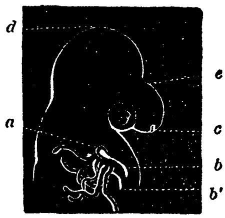
The next external change is the division of the tail-end into two caudal lobes. The notochord arises as a rod-like thickening of the third germ-layer, from which it afterwards entirely separates, so that the germ, if cut transversely, would appear somewhat as in the embryo bird (Fig. 304).

Fig. 287.



More advanced Embryo Skate.

Fig. 288.

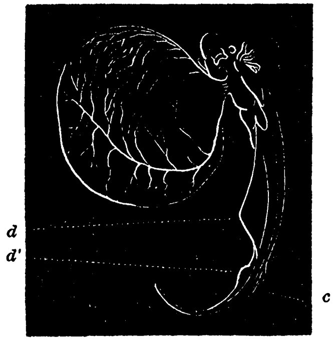


Side view of head of Fig. 287.

Now the protovertebræ arise, and about this time the throat becomes a closed tube. The head is now formed by a singular flattening-out of the germ, like a spatula, while the medullary groove is at first entirely absent. The brain then forms, with its three divisions into a fore, middle and hind brain. Soon about twenty primitive vertebræ arise, and by this time the embryo is very similar, in external form, to any other vertebrate embryo, and finally hatches in the form of the adult.

Not so, however, with the skate (*Raia batis*) as it presents an additional chapter in its life-history, discovered by Professor Wyman. Fig. 286 (this and those following after Wyman) shows the young skate resting on the large yolk-sac. It is eel-shaped, the dorsal (*c*) and (*d*) anal fins extending to the end of the tail as in the eel. Fig. 287 represents a more advanced embryo, showing at *a* and *b* the pectoral and ventral fins, and at *d*, the temporary anal. Fig. 288 is a side view of the same enlarged (*a*, first branchial fissure, largest at its outer end; this enlarged portion corresponds with the future spiracle; *b*, the inner end; the first arch is in front of the fissure; *b'*, the second fissure, in front of which is the second arch, bearing a fringe; *c*, nasal fossa; *d*, projection of the optic lobes; *e*, cerebral lobes.)

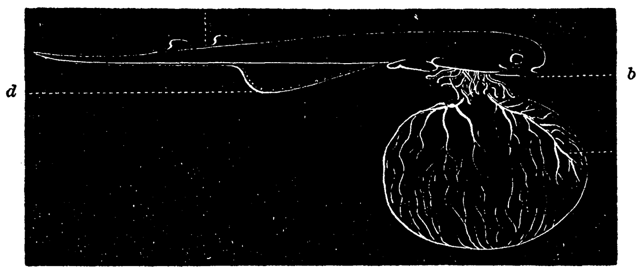
Fig. 289.



Shark-shaped embryo Skate.

Soon after the embryo skate becomes shark-shaped, as in Fig. 289, while Figs. 290 and 291, represent a lateral and dorsal view of the embryo (*b*, facial disk; *a*, pectoral; *c*, ventral fin; *e*, gill-fringes). There are at first seven branchial fissures, the most anterior of which is converted into the spiracle, which is the homologue of the Eustachian tube and the outer ear-canal; the seventh is wholly closed up, no trace remaining, while the five others remain permanently open.

Fig. 290.



More advanced embryo of Skate.

Fig. 292 represents the newly hatched skate, when the form of the adult is closely approached (*a*, yolk-sac in the cavity of the

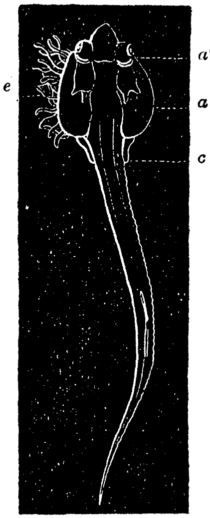
abdomen, connecting with the intestine, *b*; *c*, embryonic portion of the tail which disappears in the adult (Wyman).

A condensed summary of the chief events in the life of a Selachian, is as follows:—

1. Partial segmentation of the germinal disk.

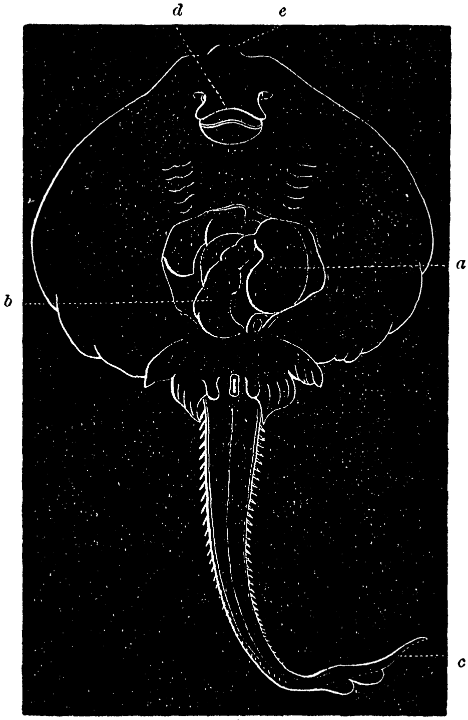
2. The embryo arises as a distinct body from the germinal disk (the "gastrula"-condition being suppressed).

Fig. 291.



Dorsal view of Fig. 290.

Fig. 292.



Newly-hatched Skate.

3. The embryo appears like that of any other vertebrate, until finally

4. The shark or skate form is assumed just before birth, or hatching from the egg.

5. The skates pass through a shark-like form, before attaining the adult shape.

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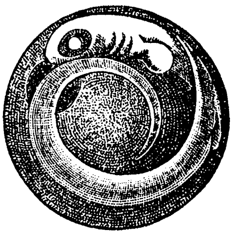
Wyman. Observations on the Development of *Raia batis*. (Memoirs Amer. Acad.

Bambeke. Recherches sur le Developpment du *Pelobates fuscus* (Mémoires couronnés Acad. Belgique, 34, 1870.)

Balfour. A preliminary Account of the Development of the Elasmobranch Fishes. (Quart. Jour. Micr. Science, 1874.)

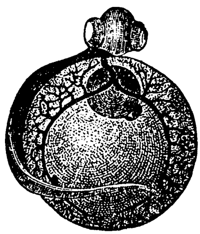
Development of the bony Fishes. During their reproductive season, the bony fishes, such as the strikleback, salmon and pike, are more highly colored than at other times, the males being especially brilliant in their hues, while other secondary sexual characters are developed. The female deposits her eggs either in masses at the surface of the water, as in the cod and goose fish, or at the bottom on gravel or sand, as in most other fishes, the male passing over them and depositing his "milt" or spermatic

Fig. 293.



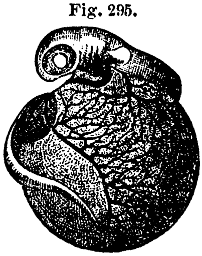
The same as Figs. 294, 295, 296, before the egg-shell has burst.

Fig. 294.



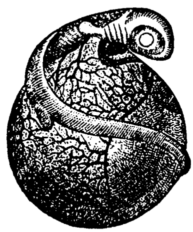
Embryo Blenny seen in front.

Fig. 295.



The same as Fig. 294, seen in profile from the right side.

Fig. 296.



The same as Fig. 294, seen in profile from the left side.

particles. The egg has a thin transparent shell, and the yolk is small, covered with a thick layer of the "white."

The eggs after fertilization undergo partial segmentation, the primitive streak, notochord, nervous cord and brain developing much as described in the section on the embryology of birds. That the embryo before us is a fish is soon determined by the absence of an amnion and allantois, and by the fact that the germ lies free over the yolk like a band. Figs. 293, 294, 295, 296 (cop-

ied by Agassiz[1] from Rathke), represent an advanced stage of the embryo Blenny (*Zoarces viviparus*) in various positions, with the eyes, gill arches, fins and vitelline network of blood vessels on the outer surface of the yolk sac.

In the pike the heart begins to beat about the seventh day, and by this time the alimentary canal is marked out. The primitive kidneys are developed above the liver. The air-bladder (probably the homologue of the lungs of higher vertebrates) arises as an offshoot opposite the liver from the alimentary canal, and the gall-bladder is also originally a diverticulum of the intestine. The urinary bladder in the fish is supposed to be the homologue of the allantois of the higher vertebrates. The principal external change is the appearance of the usually large pectoral fins.

The embryo pike hatches in about twelve days after development begins and swims about with the large yolk bag attached, and it is some seven or eight days before the young fish takes food, living meanwhile on the yolk mass. The perch hatches in twelve days after the egg is fertilized, and swims about for eight or ten days before the yolk is absorbed. The vent opens in the pike four days, and in the perch six days, after hatching. The gills gradually develop as the yolk is absorbed.

The tail in most bony fishes (the Gadidæ excepted, according to Owen), is heterocercal as in the maturer sharks, but subsequently after the fish has swam about for a while and increased in size it becomes homocercal or symmetrical. The scales are the last to be developed.

In the large size of the pectoral fins, the position of the mouth, which is situated far back under the head, the heterocercal tail, the cartilaginous skeleton and uncovered gill-slits, the embryo salmon, pike, perch, etc., as Owen observes, manifest transitory characters which are permanent in sharks (*Selachii*).

A summary of the changes undergone in the bony fishes is as follows:

1. Segmentation partial.
2. A gastrula-condition in the lamprey and sturgeon, but not in the bony fishes (trout, etc).
3. The embryo arises as in any other vertebrate.

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[1] The Structure and Growth of Domesticated Animals," 20th Ann. Report of the Secretary of the Massachu etts Board of Agriculture. Boston, 1873. These were kindly loaned by Mr. C. L. Flint, the Secretary.

4. Adult form attained at the time of hatching or birth, in the viviparous species; certain forms undergoing slight metamorphosis.

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Œllacher. Beiträge zur Entwicklung der Knochenfische, etc. (Siebold and Kölliker's Zeitschrift, 1873, '74.)

Kowalevsky, Owsjannikoff, und Wagner. Entwickelung der Störe (Sturgeon. Bulletin Imp. Acad. St. Petersburg, xiv, 1873.)

With the writings of Kupffer, Götte, Ray Lankester and Owsjannikoff.

Development of the Amphibia. Passing by the Dipnoa (Ceratodus, Protopterus and Lepidosiren) of whose development we as yet are totally ignorant, and the Simosauria, Plesiosauria and Ichthyosauria, we come to the salamanders and toads and frogs, or Amphibia. The early history of the extinct Archegosaurus, Dendrerpeton and Labyrinthodonts died with them, and we can only predicate from the imperfectly known structure of the adult forms that their young possibly developed in a manner like that of the living batrachians.

As in the fishes the batrachians are most highly colored during the breeding season. The males of certain newts acquire the dorsal crest and a broader tail-fin, aiding in the process of fecundation (Owen), and other secondary sexual features are added, especially to the male during the reproductive season. After an imperfect sexual union the salamanders deposit their eggs on the leaves of aquatic plants. The eggs of the toad are laid in long strings, those of the frog in masses. In these creatures each egg is fertilized as it is extruded, and the egg then swells greatly, the yolk appearing as a dot in the large jelly-like mass surrounding it.

Until we have a detailed embryology of the Amphibians, studied in the light of the newer school of embryology, the reader must be content with the following summary of Owen's account in his "Anatomy of Vertebrates."

The segmentation of the egg in the Amphibia is total, the process beginning usually about three hours after impregnation in the frog, and lasting twenty-four hours. The primitive streak, the notochord and nervous system then arise as in other craniated Vertebrates. After the appearance of the branchial arches, the gills begin to bud out from them, finally forming the larger gills

of the tadpole. The embryo now rests on the large yolk sac, much as in the embryo fish, but this is entirely absorbed before the embryo leaves the egg. Before the yolk-sac is absorbed a communication opens between the alimentary canal and the branchial cavity in the head (bucco-branchial cavity of Owen), "and this opens externally on the lower part of the head by a vertical fissure, on each side of which a small protuberance buds out, forming a special organ of adhesion — a pair of temporary cephalic limbs." (Owen.) Now the gills having got their growth, the remnant of the yolk enclosed by the abdominal walls, and the tail well developed, the tadpole bursts its egg membrane and swims about freely. In Italy, Rusconi found that the tadpoles hatched in four days, in England they hatch in five days, and the period may be prolonged to four weeks by cold weather. It is a common sight in Maine to see frogs' eggs laid in ponds still containing ice and snow.

The tadpole is much less developed than the larval fish or any other vertebrate; the intestine is not yet formed, and in other important characters it is lower in organization than the freshly hatched fish. It is also a vegetarian, eating decaying leaves; the mouth is small and round, the alimentary canal is remarkably long, the intestine coiled up in a spiral, the mouth is small, destitute of a tongue and the beak unarmed with teeth. "About the middle period of aquatic life the true or permanent kidneys begin to be formed from and upon the primordial ones; and the basis of the ovaria, or testes, may now be discerned. The oviduct is soon distinct from the ureter; but the testes retain the same excretory duct as the kidneys; their *vasa deferentia* communicate with retained cæca of the primordial kidneys before penetrating the later glands; the upper or anterior ends of the first remain for some time behind the heart." (Owen.)

"Soon after the external gills have reached their full development they begin to shrink, and finally disappear; but the branchial circulation is maintained some time longer upon the internal gills; these consist of numerous short tuft-like processes from the membrane covering the cartilaginous branchial arches; they are protected by the growth of a membranous gill-cover, which, as the external branchiæ are absorbed, leaves only one small external orifice, by which the branchial streams, admitted by the mouth, continue to be expelled. The chief distinction between the fully

developed branchial circulation in the Batrachian larva and that of the fish consists in the presence of small anastomosing channels, between the branchial artery and vein of each gill, proximad of the gill itself. The tongue makes its appearance when the fore limbs are developed."

The vertebræ of the tadpole are biconcave, but in the change to the adult are converted into cup-and-ball joints, by ossification of the substance of the cavities, and its coalescence either with the fore (Pipa) or back (Rana) part of the centrum. The remarkable changes in the hyo-branchial apparatus and the skull are described by Owen.

The accompanying figures (from Tenney's Zoology) represent the external changes of the toad from the time it is hatched until the form of the adult is attained. The tadpoles of our American toad, as observed in the European toad by Owen, are smaller and blacker in all stages of growth than those of the frog. The tadpole is at first without any limbs (Fig. 297) ; soon the hinder pair bud out. After this stage (Fig. 298) is reached, the body begins to diminish in size. The next important change is the growth of the front

Fig. 299.

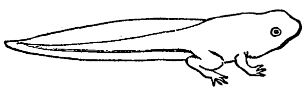


Fig. 298.

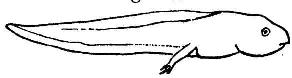


Fig. 297.

Fig. 300.

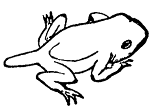


Fig. 301.

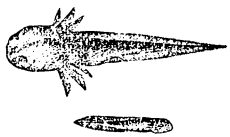
Metamorphosis of the Toad.

legs and the partial disappearance of the tail (Fig. 299), while very small toads (Figs. 300 and 301), during midsummer, may be found on the edges of the pools in which some of the nearly tailless tadpoles may be seen swimming about. When the tadpoles are hatched late, the gills are often retained through the winter, as large tadpoles of frogs are often found in pools by breaking through the ice. It is three years, according to Owen, before the Amphibia are capable of breeding.

"In the newts (Triton) the gills are in three pairs, larger and more complex than in the frog; the fore limbs are the first to

emerge, and the gills persist long after the hind limbs are developed." (Owen). While as a rule the eggs of newts or salamanders are laid in the water, the red-backed salamander lays its eggs in damp places on land, though the young are provided with gills. Fig. 302 (after Hoy) represents the young of *Amblystoma lurida* on the tenth day after hatching, the lower figure the natural size of the freshly hatched young. In the Surinam toad and Hyla of the island of Mauritius there is no metamorphosis, the young hatching with the form of the adult.

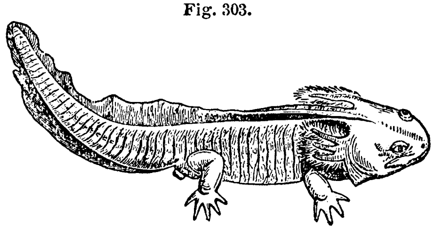
Fig. 302.



Larval Salamander.

The Siredon or Axolotl of Mexico, according to Dumeril, lays eggs, though a larva, while, as in the Axolotl, the larva of *Amblystoma mavortium*, originally described as an adult animal under the name of *Siredon lichenoides* (Fig. 303, from Tenney's Zoology) has been found by Professor Marsh to drop its gills and assume its adult form when brought to the sea level, its original habitat being the lakes situated in the Rocky Mountains at an altitude of 4,500 – 7,000 feet.

Fig. 303.



Siredon or larval Salamander.

Professor Owen has well summed up the wonderful changes undergone in these metamorphoses, which are exactly paralleled by those of the vegetarian larval gnat with biting jaws and gills into the blood-sucking volant, air-breathing fly; entirely new organs replacing the deciduous ones of the larva, and the body in attaining maturity being made over anew. "In the metamorphoses of the Batrachia," says the distinguished comparative anatomist, "we seem to have such process carried on before our eyes to its extremest extent. Not merely is one specific form changed to another of the same genus; not merely is one generic modification of an order substituted for another, the transmutation is not even limited by passing from one order (Urodela) to another (Anoura); it affects a transition from class to class. The Fish becomes the Frog; the aquatic animal changes to the terrestrial one; the water-breather becomes the air-breather; an insect diet is substituted for a vegetable one. And these changes, more-

over, proceed gradually, continuously, and without any interruption of active life. The larva having started into independent existence as a fish, does not relapse into the passive torpor of the ovum to leave the organizing energies to complete their work untroubled by the play of the parts they are to transmute, but step by step each organ is modified, and the behavior of the animal and its life-sphere are the consequence, not the cause, of the changes."

"The external gills are not dried and shrivelled by exposure to the air, nor does the larva gain its lungs by efforts to change its element and inhale a new respiratory medium. The beak is shed, the jaws and tongue are developed, and the gut shortened, before the young Frog is in a condition to catch a single fly. The embryo acquires the breathing and locomotive organs—gills and compressed tail—while imprisoned in the ovum; and the tadpole obtains its lungs and land-limbs while a denizen of the pool; action and reaction between the germ and the gelatinous atmosphere of the yolk, or between the larva and its aqueous atmosphere, have no part in these transmutations. The Batrachian is compelled to a new sphere of life by antecedent obliterations, absorptions and developments, in which external influences and internal efforts have no share."

While the passage we have quoted is an attack against Lamarckianism, we do not see but that in a long course of generations of the ancestors of the present species of amphibians, the metamorphoses may have become gradually established, finally becoming the normal history of each individual; the changes of the individual epitomizing the successive steps in the collective life-history of the entire group of Amphibians. That changes in the physical surroundings induce important modification of structure is seen in the exceptional mode of metamorphosis of the Surinam Pipa, or the Hyla of Mauritius, and on the other hand, in the prematurity of the axolotl, which near the level of the sea drops its gills, while five or six thousand feet above the sea it retains its gills and still produces young.

To recapitulate, we have the following stages of development in the Amphibia:

1. Morula (segmentation total).
2. The embryo develops as in the bony fishes.
3. Young with external gills hatching with a fish-like form, but

much less advanced in internal organization; or, rarely, hatching in the adult form, the metamorphosis being suppressed.

4. Larval forms retained as in the Menobranchus, Siren, Menopona and Salamanders; or dropped, as in the toad and frog.

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Development of the Reptiles. We now come to study the embryology of those vertebrates in which there is an important embryonal membrane, the *amnion*, developed, besides an *allantois.* The eggs of reptiles from their abundant supply of yolk cells, and the early stages of the embryo, are so much like those of birds that the reader is referred to the account of the early stages of the chick for a more complete account of the early phases of embryonic life in the reptiles.

As with birds, the eggs are enormous in size, and like those of the ostrich they are laid in the sand, and are left by the parent to be hatched by the warmth of the sun.

Professor H. J. Clark, in his "Mind in Nature," tells us that of all eggs those of turtles are by far the most easily preserved in a healthy state during the time of incubation. "All that is required to obtain them is to collect a number of turtles in early spring, before May, and keep them enclosed in some shady spot where they can have easy access to water and soft earth, and to feed them well with fresh herbage, such as plantain-leaves, lettuce, beet-leaves, etc., etc., and in the course of time, usually in May and June, they may be caught, at early dawn, digging holes in the earth with their hind legs, and depositing therein their brood of eggs, and then covering them up."

The lizards, snakes, and crocodiles, lay their eggs in sand or light soil, the iguana in the hollows of trees, while certain lizards and snakes are viviparous. Agassiz has discovered the extraordinary fact that in turtles fecundation does not appear to be an instantaneous act, resulting from one successful connection of the sexes, as it is with most animals, but "a repetition of the act, thrice every year, for four successive years, is necessary to determine

the final development of a new individual, which may be accomplished in other animals by a single copulation." From the same source we learn that *Chrysemys* (Emys) *picta* does not lay its eggs before the eleventh year. Our other turtles probably lay their eggs from the eleventh to the fourteenth year, according to the species. The operation takes place in the month of June, both at the north and south, climatic differences not seeming to have any effect upon this particular function.

Before segmentation of the yolk the nucleus, or germinal vesicle, undergoes self-division. According to Agassiz and Clark "this takes place, at least to a certain extent, without the influence of fecundation within a year, but at the same time has been seen only in those eggs which have been expelled from the ovary. Finally they become the original cells, "the primitive embryonic cells" engaged in the composition of the different organs of the body. In the bony fishes, according to Œllacher, the germinal vesicle is ejected bodily from the germinal disk, and Foster and Balfour think this fate awaits that of the birds. In insects the germinal vesicle is supposed to undergo self-division and form the nuclei of the cells of the blastoderm.

The segmentation of the yolk has been fully observed in *Glyptemys* (Emys) *insculpta*. The process of segmentation is not so regular, and there does not seem to be always, in the beginning, a symmetrical halving of the embryonic area, as has been observed among birds; but in other respects it resembles what takes place within the eggs of the latter animals, and finally results in shaping out the embryonic disk." Agassiz and Clark, from whom we have quoted, think, however, that, from certain phenomena observed by them, the whole mass of the yolk becomes segmented.

The formation of the primitive streak, the amnion, allantois, and *chorda dorsalis*, are much as observed in the chick, and for an account of the early stages of the embryo reptiles, the reader is referred to the chapter on the embryology of birds. The lungs arise as hollow sacs projecting from the sides of the throat; the liver is a thickening of the same membrane from which the stomach is formed, while the reproductive glands "arise in intimate connection with the posterior end of the intestine."

By the time that the heart has become three-chambered, the vertebræ have reached the root of the tail, the eyes have become entirely enclosed in complete orbits, and the allantois begins

to grow. Soon after, the embryo turns upon its axis, and always rests on its left side. The nostrils may now be recognized as two simple indentations at the end of the head, and at first are not in communication with the mouth, but soon a shallow furrow leads to it.

The shield begins to develop by a budding out laterally of the musculo-cutaneous layer along the sides of the body, and the growth of narrow ribs extending to the edge of the shield. "The feet, or rather paddles, of the lower forms of turtles, the Chelonioidæ, do not remain in a partially undeveloped state, as might be expected from what is observed among other vertebrates, but undergo what may be called an excess of development; the bones of the toes becoming very much elongated, and the web—which remains soft among some turtles with moderately elongated toes, —is hardened by the development of densely packed scales, so that the whole foot is almost as rigid as the blade of an oar. At this time the embryo of *Chelydra serpentina* snaps at everything which touches it.

Of the development of the Saurians, or lizards, we have no complete account. The advanced embryo of the lizard, as figured by Owen (443), is like that of the turtle without its shell.

As regards the development of snakes, Owen, deriving his information from Rathke's work, tells us that in the oviparous snakes (*Natrix torquata*) the embryo partially develops before the egg is laid, while the young hatches in two months after the egg is deposited. By this time the amnion is perfected, "the head is distinct, and shows the eye-ball and ear-sac; also the maxillary and mandibular processes. The allantois is about as large as the head." The long trunk of the serpent grows in a series of decreasing spirals, and when five or six are formed, the rudiment of the liver and the primordial kidneys are discernible." At the latter third of embryonic life the right lung appears as a mere appendage to the beginning of the left.

A summary of the changes in the egg undergone by the reptiles is as follows:

1. Segmentation partial, possibly total (morula?).
2. The embryo develops much as in the bony fishes until the embryonal membranes appear.
3. Formation of an amnion.
4. After the alimentary canal is sketched out, the allantois buds out from it.

5. The shield of the turtle develops and the reptilian features are assumed.

6. The embryo hatches in the form of the adult, there being no metamorphosis.

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Development of Birds. So much alike are all the living species of birds that the embryology of a single kind is in all probability a type of that of the others. The development of the domestic fowl has been studied in more detail than any other vertebrate, since it is easy to hatch the eggs artificially, and from their large size they can be examined more readily than the eggs of fishes. Our account of the embryology of birds will be taken from the admirable account by Foster and Balfour in their "Elements of Embryology," and we shall freely use their work, often quoting them, word for word, where it is not possible to farther condense their language.

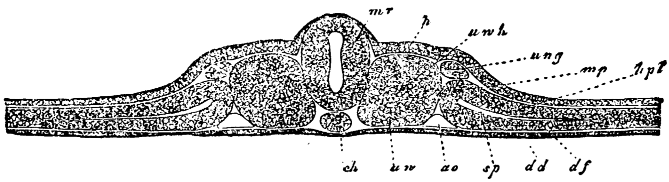
The eggs of the hen are fertilized in the upper extremity of the oviduct, whether before or after the "white" of the egg is deposited is unknown, but at any rate before the shell is deposited around the "white."

First day. As the first result of impregnation the germinal vesicle disappears, probably being, judging from the analogy of the bony fishes, bodily ejected from the germinal disk. Then begins the process of segmentation of the yolk, which goes on at about the time the shell is formed. Segmentation is partial, being restricted to the germinal disk of the ovarian egg; the result is the formation of the blastodermic disk, which is the beginning of the embryo, resting on the upper surface of the yolk and appearing as a pale round spot seen in the freshly laid egg. This blastoderm at first consists of two layers of cells, the upper made up of nucleated cells, and the lower of irregular rounded masses called "formative cells."

Now begins the marking out of the embryo, which develops in the "*area pellucida*" a transparent rim (encompassed by the "*area opaca*") surrounding the blastoderm. The first step is the origin of an inner germ-layer, the two others having previously

arisen, so that we now have the three germ-layers found in all vertebrates and in some invertebrates. From the outer layer (epiblast) arises the tegument and walls of the body, with the nervous cord; while from the second (mesoblast) are formed the heart and the vascular system or blood-vessels, and the stomach and intestines. The third and innermost layer is called the "hypoblast." By the sixth or eighth hour these three membranes become definitely established. The middle layer now thickens and thus causes the appearance known as the "primitive streak," along the middle of which runs the depression known as the "primitive groove." In front of the primitive groove appears the "medullary groove," and below it the notochord or "*chorda dorsalis*" originates from the cells of the middle layer. This notochord (Fig. 304, *ch*) lies directly beneath the medullary tube

Fig. 304.



Section of an Embryo Hen.

(*mr*) and between the outer and third germ-layer in the form of a flattened circular rod. The blastoderm is now folded anteriorly like the letter S; this is called the "head-fold," and soon after the "tail-fold" is formed in a similar way. These two folds meet in the middle thus forming the body of the embryo.

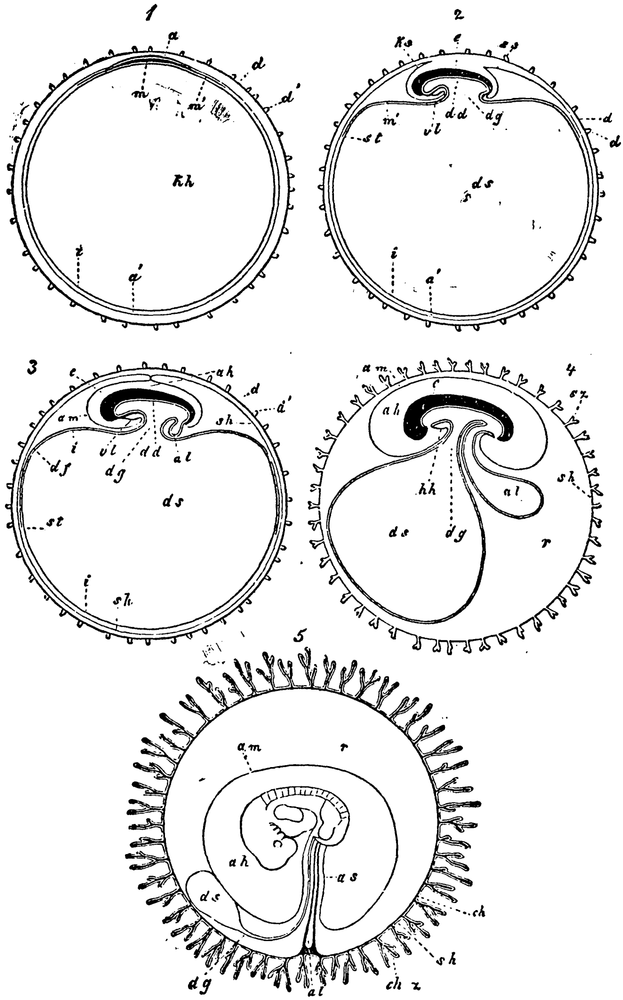
Next the primitive groove and streak disappear as the sides of the medullary groove rise up, when they finally meet, forming the neural tube, or hollow in which the nervous cord is formed.

About this period the first pair of protovertebræ make their appearance. They arise from the mesoblast as two cubical masses (Fig. 304[1], *u w*) lying one on each side of the notochord. Two more pairs appear behind the first pair before the first day is

[1] Fig. 304; *dd*, third or inner germ-layer (darmdrüsenblatt or hypoblast); *ch*, *chorda dorsalis* or notochord; *uw*, primitive vertebræ, or protovertebræ; *uwh*, cavity in the protovertebræ; *ao*, primitive aorta; *ung*, Wolffian duct; *sp*, split in the middle-germ layer, the beginning of the pleuro-peritoneal cavity (mesoblast) by which it is divided into two layers, the lower layer (*df*) the splanchnopleure (or darmfaserplatt), the upper layer (*hpl*) being the somatopleure (hautplatt), the two layers unite at *mp* (Kölliker's mittelplatt); *mr*, medullary tube (rückenmark); *h*, outer germ-layer (hornblatt or epiblast).

ended. "Out of the protovertebræ are formed not only the permanent vertebræ, but also the superficial dorsal as well as certain

Fig. 305.



Early stage of a Vertebrate (Fowl).

other muscles and the spinal nerves. The pair of protovertebræ first formed corresponds not with the first cervical vertebra of the adult chick, but rather with the third or even fourth; for though

the majority of the protovertebræ are formed regularly behind the first pair, two or even three pair may make their appearance in front of it" (Foster and Balfour).

Fig. 304 (from Kölliker) is a cross section through an embryo chick of the second day magnified 90–100 times, showing the relations of the medullary tube, *chorda dorsalis* and protovertebræ.

Meanwhile the middle layer has split into two layers; the upper (or outer) leaf is called the "somatopleure," so-called from its giving rise to the body walls, while the lower (or inner) leaf is called the "splanchnopleure," as it is destined to form the alimentary canal, and the liver and other glands originating from the digestive cavity.

The amnion next arises from certain folds of the somatopleure. As the embryo thickens and sinks into the yolk two folds grow out of the head and tail end respectively (Fig. 305, 2, *ks* and *ss*). These finally meet and coalesce on the fourth day over the back of the embryo, forming the amniotic cavity (Fig. 305, 3, *ah*) in which the embryo lies. The fluid which fills this cavity is called the amniotic fluid.

The allantois arises as an appendage of the alimentary canal, budding out at the hinder end of the embryo. It finally grows (as in Fig. 305, 4, *al*) so large as to curve over the embryo, serving as a fœtal respiratory organ.[1]

Second Day. By the time the embryo is thirty hours old the outlines are bolder, more distinct and the tissues firmer, so that

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[1] Fig. 305. Five schematic figures showing the development of the fœtal egg-membranes, where in all except the last the embryo is represented as if seen in longitudinal section. 1. Egg with *zona pellucida* (embryonic sac) blastoderm (*a*, *l*) germinal disk and embryo. 2. Egg with the first traces of the yolk sac (*d*) and amnion (*ks*. *ss* and *am*). 3. Egg with the amnion uniting and forming a sac; the allantois (*al*) budding out. 4. Egg with the vili of the serous membrane (*sz*); the allantois larger; embryo with mouth and anal opening. 5. Egg in which the vascular layer of the allantois lies close to the serous layer and has grown into the villi of the same, constituting the true chorion (*ch*). Yolk sac much smaller, about to be drawn into the cavity of the amnion.

d, yolk-skin; *d'*, villi of the yolk-skin; *sh*, serous membrane: *sz*, villi of the serous membrane: *ch*, chorion (vascular layer of the allantois) *chz*, true villi of the chorion (arising from the projections of the chorion and the sac of the serous membrane); *am* amnion; *ks*, head-fold of the amnion; *ss*, tail-fold of the amnion; *ah*, cavity of the amnion; *as*, sheath of the amnion for the navel string; *a*. the first beginning of the embryo arising from a thickening of the outer layer of the blastoderm *a'*; *m*, thickening forming the germ in the middle layer of the blastoderm (*m'*), which at first only reached as far as the germinal disk, and afterwards forms the vascular layer of the yolk-sac (*df*) which connects with the intestino-muscular layer (darmfaserplatte); *st*, *sinus terminalis*; *dd*. intestino-glandular layer (darmdrusenblatt) arising out of a part of *i*, the inner layer of the blastoderm (afterwards the epithelium of the yolk-sac; *kh*, cavity of

the whole blastoderm can be removed from the egg with much greater ease than before. The head-fold has now become more prominent than before. The nerve-tube, at first of uniform thickness dilates anteriorly forming the first cerebral vesicle, and the second and third cerebral vesicles successively form, the protovertebræ increase rapidly, and soon the embryonic chick presents the appearance of the embryo rabbit of nearly the same age.

The alimentary canal commences as a *cul de sac*, closed in front but widely open behind, situated below the anterior end of the medullary tube. The heart originates also in the head-fold at about the time the protovertebræ are formed, and the rudiment is situated below the fore gut or rudiment of the alimentary canal; by the end of the first half of the second day it is flask-shaped, with a slight bend to the right. "Soon after its formation the heart begins to beat, its at first slow and rare pulsations beginning at the venous and passing on to the arterial end." Its movements begin before the cells of which it is composed are differentiated into muscle or nerve-cells. To provide channels for the fluid pressed out by the contractions of the heart, the heart divides into the two primitive aortæ, and connects with other embryonic temporary arteries and veins. Meanwhile in the vascular area and *area pellucida*, the arteries, capillaries and veins rapidly develop, and blood disks arise as amœba-like cells separating from the adjacent cell-mass of the mesoblast (middle germ-layer), while the vessels are contemporaneously forming; the red blood corpuscles not being true cells, but nuclei. The first half of the second day ends with the rise of the rudiment of the Wolffian duct. "It is important to remember that the embryo of which we are now speaking is simply a part of the whole germinal membrane, which is gradually spreading over the surface of the yolk. It is important also to bear in mind that all that part of the embryo which is in front of the most anterior protovertebræ corresponds to the future head, and the rest to the neck, body and tail. At this

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the blastoderm, which afterwards becomes *ds*, the cavity of the yolk-sac; passage way of the yolk; *al*, allantois; *e*, embryo; *r*, original space between the amnion and chorion, filled with albuminous fluid; *vl*, anterior body-wall in the region of the heart; *hh*, cavity of the heart without the heart itself.

In Figs. 2 and 3, the amnion is for the sake of clearness represented as situated too far away from the embryo; so also the cavity of the heart is drawn too small and the embryo too large, since except in Fig. 5, they are only drawn diagrammatically. These and Fig. 304, from Kölliker's Entwickelungsgeschichte des Menschen und der hoheren Thiere.

period the head occupies nearly a third of the whole length of the embryo" (Foster and Balfour).

In the second half of the second day, among the most important changes are the appearance of the second and third cerebral vesicles, the optic vesicles, while the "first rudiment of the ear is formed as an involution of the epiblast on the side of the hind brain or third cerebral vesicle."

Third day. This day is one of the most eventful, as the rudiments of so many important organs now first appear. First, the embryo, now almost completely enveloped by the amnion, turns around so as to lie on its left side. The heart, originally formed under where the brain is destined to lie, moves backward into the trunk, and by this time (the third day) the neck has been formed, in which appears the four branchial fissures, the most anterior being formed first. It is these temporary fissures which correspond to the branchial fissures of Amphioxus. "On account of this resemblance—in fact by some assumed as an identity both in form and function—the fissures have been called by embryologists the *branchial fissures* (compare Fig. 288) and the vessels [passing between them] the branchial aortæ, the former corresponding with the passages between the gills of fishes, and the latter with the vessels which supply the gills with blood" (Clark's Mind in Nature, p. 311).

In fact the embryo bird in some respects is now as far advanced in organization as the Lancelet, and may be rudely compared with that animal, though the incipient neck, head and brain are features which the Lancelet lacks.

The eye commences as a lateral outgrowth of the fore brain, in the form of a stalked vesicle subsequently converted into the optic nerve, while the lens is formed by an involution of the skin of the body (outer germ-layer) over the front end of the optic vesicle. The ear is also at first simply an involution of the outer germ-layer (epiblast) forming a pit, or "otic vesicle," which is destined to form the internal ear, containing the bones and other parts of the inner ear. The nose begins as two shallow pits formed by the sinking in of the outer germ-layer. Each of these pits is situated next to the olfactory vesicles (afterwards nerves), but at first there is no connection between the pits and the nerves as between the pits and the mouth, which is in fact not yet formed, since it arises afterwards as an extension inward of the cleft be-

tween the first branchial folds and its branch, as the jaws or maxillæ arise from the first fold, the upper jaws being two branches of the fold, the fold itself being the under jaw, while a lozenge-shaped cavity between the fold and its branches becomes the mouth.

Meanwhile, for all the changes in the different organs are going on contemporaneously, the vesicles or lateral expansions of the nerve-tube appear, the vesicles of the cerebral hemispheres developing, as well as the separation of the hind-brain into the cerebrellum and *medulla oblongata*. The digestive cavity is during the third day also, differentiated into the fore-gut and hind-gut, the former farther subdividing into the œsophagus, stomach and duodenum, and the hind-gut into the large intestine and cloaca. The lungs arise as two pocket-like appendages of the alimentary canal immediately in front of the stomach; while the liver is originally two diverticula, and the pancreas a single offshoot from the duodenum.

Fourth day. With a decided increase in size by this day, the amnion becomes more distinct, and the allantois is visible. The wings and legs now appear as flattened conical buds arising from the "Wolffian ridge," a low ridge running from the neck to the tail, those forming the wings being scarcely distinguishable from the rudimentary legs.

The olfactory grooves appear at this time and the partition heretofore existing between the mouth and throat is absorbed and disappears.

The protovertebræ have, by this time, increased in number from thirty to forty. The upper portion (muscle-plate) having previously separated to form the muscles inserted in the skeleton (episketal muscles of Huxley), has left the remainder of each protovertebra as a somewhat triangular mass, the upper angle of which grows up and meets its fellow in the median line above, thus enclosing the nerve-canal. On the lower side each protovertebra sends out a similar growth enclosing the notochord. "While the inner portion of each protovertebra is thus extending inwards around both notochord and neural canal, the remaining outer portion is undergoing a remarkable change. It becomes divided into an anterior or præaxial, and a posterior or postaxial segment. The anterior, which is the larger and more transparent of the two, is the rudiment of the spinal ganglion and nerve, while the pos-

terior, which remains more particularly connected with the extensions round the neural canal and notochord, goes to form part of the permanent vertebra. In this way each protovertebra, having given rise to a muscle-plate, is farther subdivided into a ganglionic rudiment, and into a mass which we may speak of as a 'primary' vertebra, consisting as it does of a body or mass investing the notochord, from which springs an arch covering in the neural canal." (Foster and Balfour.) The conversion of the primary vertebræ or membranous vertebral column into the permanent vertebræ is "complicated by a remarkable new or secondary segmentation of the whole vertebral column," so that "each permanent vertebra is formed out of portions of two consecutive protovertebræ. Thus, for instance, the tenth permanent vertebra is formed out of the hind portion of the tenth protovertebra, and the front portion of the eleventh protovertebra, while its arch, now attached to its front part, was attached to the hind part of the tenth protovertebra." (Foster and Balfour).

By the sixth day the notochord begins to diminish and disappear by the time the bird is hatched, while by the twelfth day the ossification of the bodies of the vertebræ commences, the process beginning in the second or third cervical, and thence extending backwards. The ribs begin as a downward growth from the exterior of the vertebra, at first separate from the bodies of the vertebra.

Between the eightieth and one hundredth hour of incubation the permanent kidneys arise, and previous to this the sexual glands have arisen out of the middle germ-layer, from the germinal epithelium lying at the upper end of the pleuroperitoneal cavity. In this epithelium may be seen certain large cells, the primordial ova, which are at first seen in male as well as female embryos, so that in early stages it is impossible to distinguish the sexes. Between the eightieth and one hundredth hour, however, the primordial ova disappear in those embryos destined to be males, while they enlarge and multiply in the female. "The large nucleus of the primordial ovum becomes the germinal vesicle, while the ovum itself remains as the true "ovum." The testes begin to arise on the sixth day.

Fifth day. This period is signalized by the futher growth of the allantois, and by the appearance of the knee and elbow, and of the cartilages which precede the formation of the bones of the

digits and limbs; as well as the formation of the primitive skull, with the development of the parts of the face, and the formation of the anus.

The cranium, from the researches of Rathke, Parker and others, is formed from the middle germ-layer, and in the fourth day is simply membranous; after that time the tissue composing it becomes cartilage. After the fourth day the primitive skull consists of two portions, *i.e.*, a sheet of cartilage ensheathing the notochord from its anterior end to the first vertebra. "This sheet of cartilage forms an *unsegmented* continuation of the vertebral bodies. It is to be considered as the most anterior portion of the axial skeleton, in which the segmentation has become obliterated; and as such is equivalent not to one, but to a (hitherto not certainly determined) number of vertebræ." (Foster and Balfour. For the farther changes in the development of the skull the reader is referred to Parker's memoir on the Development of the Skull of the Common Fowl, or the excellent, illustrated abstract in Foster and Balfour's "Elements.")

Not until the sixth day are distinct bird-characters developed. Hitherto it would be almost impossible to distinguish the embryo from a reptile or mammal. During the sixth and seventh day the wing and foot assume a bird form, the crop and intestinal cœca make their appearance, "the stomach takes the form of a gizzard, and the nose begins to develop into a beak, while the incipient bones of the skull arrange themselves after the avian type. . . . From the eleventh day onwards the embryo successively puts on characters which are not only avian, but even distinctive of the genus, species and variety." By the ninth or tenth day the feathers originate in sacs in the skin, these sacs by the eleventh day appearing to the naked eye as feathers, the sacs however remaining closed as late as the nineteenth day, though many are an inch in length.

The nails and scales begin to appear on the thirteenth day. "By the thirteenth day the cartilaginous skeleton is completed, and the various muscles of the body can be made out with tolerable clearness. Ossification begins, according to Von Baer, on the eighth or ninth day by small deposits in the tibia, in the metacarpal bones of the hind-limb, and in the scapula. On the eleventh or twelfth day a multitude of points of ossification make their appearance in the limbs, in the scapular and pelvic arches, in the

ribs, in the bodies of the cervical and dorsal vertebræ, and in the bones of the head, the centres of ossification of the vertebral arches not being found till the thirteenth day."

While the blood is at first aerated by the allantois, and there is a partial double circulation of the blood, as soon as respiration begins a completely double circulation is formed.

After the sixth day muscular movements of the embryo probably begin, but they are slight until the fourteenth day, when the embryo chick changes its position, lying lengthways in the egg, with its beak touching the chorion and shell membrane, where they form the inner wall of the rapidly increasing air chamber at the broad end. On the twentieth day or thereabouts, the beak is thrust through these membranes, and the bird begins to breathe the air contained in the chamber. Thereupon the pulmonary circulation becomes functionally active, and at the same time blood ceases to flow through the umbilical arteries. The allantois shrivels up, the umbilicus becomes completely closed, and the chick piercing the shell at the broad end of the egg with repeated blows of its beak, casts off the dried remains of allantois, amnion and chorion, and steps out into the world." (Foster and Balfour).

A brief summary of the changes undergone by the developing chick will be seen to be nearly identical with that of reptiles:

1. Partial segmentation of the yolk.
2. The embryo develops much as in the bony fishes until the embryonal membranes appear.
3. Formation of an amnion.
4. After the alimentary canal is sketched out, the allantois buds out from it.
5. The avian features appear from the sixth to the tenth day.
6. The embryo leaves the egg in the form of the adult, and like the reptile, is at once active, feeding itself.

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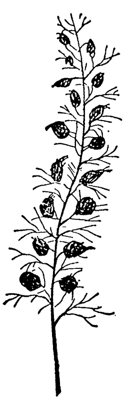
PLANTS THAT EAT ANIMALS.[1]

BY MRS. MARY TREAT.

THE Bladderwort is a common plant, growing in shallow ponds and swamps; Dr. Gray in his "Manual of the Botany of the United States," describes twelve species found within this range, and almost every muddy pond contains one or more of them. Some grow wholly or nearly out of water; but the species which I am about to describe are immersed, with finely dissected leaves on long stems floating in the water. Scattered among the leaves, or along the stems which are destitute of leaves, are numerous little bladders, the use of which we had supposed was to float the plant at the time of flowering. The flowering stems of most of the species are smooth and free from leaves or bladders, and shoot up straight from the water to a hight of from three to twelve inches, bearing at the top from one to ten curiously-fashioned flowers of a yellow or purple color. It has always been taken for granted that these little bladders were made to float the plant, although I had noticed that the stems most heavily laden with bladders sank the lowest in the water.

Fig. 306.



A portion of the stem, showing bladders. Natural size.

About a year ago (in Dec. 1873), a young man, now at Cornell University, and myself, on placing some of the bladders under the microscope, noticed animalcules—dead entomostraca, etc., apparently imprisoned therein. But our attention was not sufficiently

[1] This reprint with some alterations from the "New York Tribune," has been delayed until the publication of Mr. Darwin's last book gives fresh cause for its appearance. We are indebted to the "Tribune" for the use of the illustrations.